THE VARIATIONS AND MUTATIONS OF THE INTRODUCED LITTORINA.

A THIRD CONTRIBUTION TO THE STUDY OF VARIATION.

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THE observations recorded in this communication were made for the purpose of ascertaining additional facts relative to the variability of "introduced species," and with the design of eliciting further evidence in corroboration of certain conclusions which had been reached after an examination of a large number of eggs of the English sparrow (Bumpus, '98).

The periwinkle, *Littorina littorea* Linné, is "extremely common" among stones and on the rocks of the British shores, and is reported from Greenland, the White Sea, and the European coast as far south as Lisbon (Jeffreys, '65). Along the New England shore it is by far the most abundant mollusc at the present time. Stones, piles, and seaweed are everywhere dotted with the dark-colored shells which often form a distinct band near high-water mark.

When the tide is low, the snails often lose their hold and roll from the slanting rocks into hollows, where they may be scooped up by the handful. At Seaconnet no less than 2500 shells were taken from a small depression not more than a foot square.

The history of the introduction and distribution is as follows :

In 1841 Gould published his *Report on the Invertebrate Animals of Massachusetts*, but no mention was made of the present species.

In 1855 Morse received specimens from Bathurst, on the Bay of Chaleur, an inlet of the Gulf of St. Lawrence (Morse, 1880).

In 1870 Binney revised Gould's *Report*, gave a description of the species, and mentioned the shell as reported from Halifax

by Willis. He evidently had no idea that the Massachusetts shore was soon to be invaded. In the same year Mr. Charles B. Fuller, curator of the Portland Society of Natural History, found a few specimens in Maine at Portland and at Kennebunk (Morse, '80).

In 1871 the species was found at Hampton Beach, New Hampshire (Gray, '79).

In 1872 Professor Morse found it at Salem (a single specimen), and Verrill ('80) found it " very rare " at Provincetown, Mass.

In 1875 two specimens were taken at Woods Holl, Mass. (Verrill, '80).

In 1880 Prof. S. I. Smith found the first specimen at New Haven.

At all of these localities the shell became abundant in a very few years after its first appearance.

Thus the history of the introduction, the rapid dispersion and the remarkable increase of the periwinkle are not essentially different from that of the introduction, dispersion, and increase of the sparrow.

It is, of course, well known that *Littorina littorea* is, on its native shore, like many gasteropods, subject to variation (Jef-

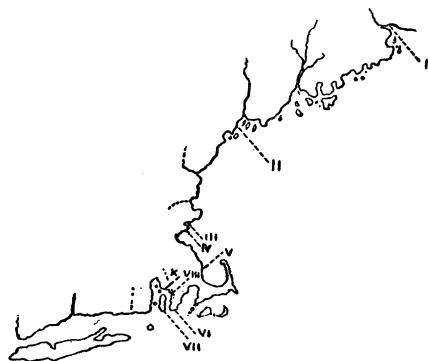FIG. 1. — Coast line of New England, indicating the localities from which collections of *Littorina littorea* have been made. I, St. Croix River; II, Casco Bay; III, Beverly; IV, Nahant; V, Plymouth; VI, Seaconnet; VII, Newport; VIII, Bristol; IX, Bristol; X, Warren River.

freys, '65). Jeffreys gives the diagnostic characters of four " varieties," though these are not characterized by definite

geographical limits, and at least two are admitted to be " perhaps monstrous rather than varietal forms."

Of the 3000 British shells which I have examined, 1000 are from Tenby, Pembrokeshire, southwest coast of Wales, 1000 from South Kincardineshire, east coast of Scotland, and 1000 from the Humber District on the east coast of England — three localities widely separated geographically, and characterized by different geological formations.   Ten thousand American shells have been collected from the ten stations indicated on the annexed map, 1000 shells being considered sufficient to represent any given locality.

The First Test of Variability.

A most superficial examination of the complement of shells (1000) from any locality shows that certain individuals are relatively longer and others are relatively shorter (ventricose)
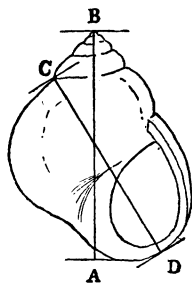
FIG. 2. — Diagram of shell to illustrate the points at which measurements were taken.

than the majority of their companions.   The ratio of breadth to length, then, is variable, and may be exactly measured and mathematically expressed.   A shell which has a breadth equal to eight-tenths the height may be indicated by 80%; one whose breadth is nine-tenths the height, by 90%; and one whose breadth equals the height, by 100%.   The distance from A to B, Fig. 2, is taken as the height, and from C to D as the breadth of the shell.   These distances were selected because they were more easily measured than the actual diameters.   A measuring instrument gave the ratio of breadth to height, *i.e.*, the index of stature, without the labor of computation.

The measurement of 1000 shells from Tenby, Pembrokeshire, Wales, reveals the following facts : The breadth of the most elongated shell is 83% of the height. The breadth of the most ventricose shell is 98% of the height. There are four shells having an index of stature of 84%, four of 85%, twenty-five of 86%, thirty-eight of 87%, etc.

Chart I.[1] — If from these data we construct a "curve of frequency," it is evident that the *location* of the curve upon the base line indicates the general shape of the shells from Tenby. The *length* of the base line, inclosed by the limbs of the curve, is an index of the amplitude of variation in respect to stature of the 1000 shells, and may be numerically expressed as 15 $(98 - 83 = 15)$. The *altitude* of the curve is an expression of conservatism, *i.e.*, it represents the segregation of the shells around a mean; and the flowing trend of the curve is at once an indication that a sufficient number of individuals has been collected to be of statistical value, and that the tension which tends to draw varieties away from the mean is constant.

Chart II. — If we now examine the curve of distribution of 1000 shells from South Kincardineshire, Scotland, we note that it lies further to the left; *i.e.*, the shells are more elongated, though its altitude and flowing trend are not considerably different from those of Chart I. The amplitude of variation, however, is slightly less, being represented by 14 $(95 - 81 = 14)$.

Chart III. — The curve of distribution for 1000 shells from the Humber District, while having practically the same altitude and the same flowing trend as curves I and II, and resting at a mean position upon the base line between the ordinates of 85% and 97%, presents, nevertheless, extreme fixity — the amplitude of variation being indicated by only 12 $(97 - 85 = 12)$. This remarkable constriction of the base line gives a precipitous appearance to the curve which Charts I and II do not have, and indicates a striking paucity in examples which depart, even a little, from the ideal mean.

[1] The subdivisions of the base line from left to right represent the grades of increase in ventricosity expressed in per cents, *i.e.*, by indices of stature. The length of the ordinates represents the number of individuals of each grade.

Let us now examine the curves of distribution of the American shells, and see if a new environment has wrought any change.

Chart IV. — This chart is based on an examination of 1000 shells from the St. Croix River in Maine, and, while it does not rest on the base line in an extreme position, its general trend and the width of its base are very different from any of the British curves.   The index of stature varies from 84% to 102%, giving an amplitude of 18 (50% greater than that given by the Humber shells), though the regular trend of the flaring base is still an indication of some continuously active law.   If a larger number of shells of the complement have departed from the ideal and have presented more extreme types of elongation on the one side and of ventricosity on the other, the shells of *mean* stature must have been depleted, and the St. Croix curve is consequently less precipitous than any of the British.

Chart V. — This chart is based on an examination of 1000 shells from Casco Bay.   The position of the curve indicates a general tendency towards ventricosity.   There are but twenty-two shells the index of which is below 88%, while there were among the South Kincardineshire collection 440 examples.   The altitude and general configuration of the present curve is not unlike curve IV, and the amplitude of variation of stature, as indicated by the breadth of base, is but slightly greater; *viz.*, 19 (103 — 84 = 19).

Chart VI. — On this chart 1000 shells from Beverly, Mass., have been tabulated.   Beverly is located at the mouth of a small inlet, ninety miles southwest of Casco Bay.   The curve is typically American, the base indicating an amplitude of variation of 20 (102 — 82 = 20), an amount far in excess of the most variable British shells.   It is worthy of note that the right limb of the curve is much less abrupt in its descent and longer in its course than the left, a feature which also distinguishes the other American curves thus far examined.   The significance of this character will be considered later on.

We have now examined 3000 British and 3000 American shells, with the result that in every case the latter are more

variable, and, if it be objected that by chance we have selected British shells from localities where they are *least* variable and American shells from localities where they chance to be *most* variable, the objection is met, if the same results follow upon the examination of a more representative collection of shells from either locality.   Let us continue, and see if it is possible to find a single American locality where the variation is restricted even to that of the most variable British series.

Chart VII. — One thousand shells from Nahant, a rocky promontory lying about ten miles south of Beverly and bathed by the cold waters of the Atlantic, yield another characteristic American curve, of low altitude and of broad base.   The index of the amplitude of variation is 19 ($102 - 83 = 19$), again in excess of that of the British shells.   The right limb is less precipitous than the left, but not so obviously as in previous cases.

Chart VIII. — This chart represents the distribution of 1000 shells from Plymouth, Mass.   While the Littorinas of Nahant were subject to the continual beating of the waves, those collected at Plymouth were from the wharves of a sandy harbor, far removed from the boisterous sea.   The curve is peculiar in that 213 shells, occurring at the ordinate of 90%, have caused an abrupt break in its contour, and formed a prominent spire to what would otherwise be a characteristic American curve. The ascent of the left limb is again considerably more abrupt than the descent of the right, and the amplitude of variation (17) is clearly American.

Chart IX. — In the warmer waters of the southern shores of New England, at the rocky headland of Seaconnet, Littorina actually swarms.   The curve of distribution, though drawn far to the left and indicating tall, elongated shells, has, nevertheless, the characteristic American contour, low altitude, flaring base, and the ascent on the left more abrupt than the descent on the right.   The amplitude of variation is as great as it was for the shells from Beverly; *viz.*, 20 ($100 - 80 = 20$).

Chart X. — Six miles to the west of Seaconnet, and largely of the same geological formation, are the equally rocky promontories of Newport.   The temperature and salinity of the water, the oceanic currents, the force of the waves, the facies

of the marine fauna and flora in these two localities are appar-
ently the same, and the Newport curve is not materially unlike
the Seaconnet curve, though its amplitude of variation, owing
to the lack of individuals presenting extreme elongation, is two
degrees less.   The ventricose shells are about evenly divided
in the two localities.

Charts XI and XII. — Bristol Narrows lies at the mouth of the
Kickemuet River, about seventeen miles north of Newport. The
water, though sufficiently salt to enable starfish to flourish, is
of somewhat less specific gravity than at Newport or Seaconnet.
Two sets of shells were examined.   One complement of 1000
was taken at a shingle beach, from among stones ranging from
the size of one's fist to that of one's head ; the other series
was collected at a spot only a few hundred feet distant, where
the animals were living upon the sand and mud.   The two
curves are remarkably alike; they are located at the same place
on the base line, between the ordinates of 83 and 101, and thus
have the same amplitude of variation; *viz.,* 18.

Chart XIII. — The shells tabulated on this chart were col-
lected at the mouth of the Warren River at a point about three
miles from Bristol Narrows.   They form a perfectly typical
American curve with abrupt ascent, low summit, and sweeping
descent.   The amplitude of variation is 20, and the curve lies
between the ordinates of 84 and 104.

Thus we have examined shells from ten American localities,
and in every case we have found that their amplitude of varia-
tion is in excess of the most variable British shells, and we
conclude that at any locality along the American coast the
shells will probably exhibit a greater variation in respect to
stature than at any locality along the British coast.

A Second Test of Variability.

It is quite possible that the American shells may be more
variable in respect to stature and still be less variable in
respect to other characters.

In the previous section it was shown that in each American
locality the shells vary through a greater amplitude than in

any British locality; but do the extremes of variation of the American shells from *all* localities equal or exceed the extremes of variation of the British shells from *all* localities ? With the data at hand it is possible for us to arrive at a reasonably certain conclusion, though to answer the question with absolute certainty one should have a very large and representative collection of shells from many localities in both countries.

The most elongated shell among the British series was collected at Kincardineshire. Its index is 81. The most elongated American shell was collected at Seaconnet, and its index is 80. While the most ventricose British shell has an index of 98 (*vide* Chart I), the most ventricose American shell has an index of 104 (*vide* Chart XIII). The most extreme cases of variation in stature are, then, presented by the American shells. This is quite a different thing from extreme amplitude of variation in particular localities, and, while it may result from the fact that a larger number of American localities have been examined, it seems hardly probable, from the data at hand, that an equal number of British localities would yield an equal number of such extreme variations.

The British shells from three localities taken at random gather in 17 grades, from 81% to 98%. The American shells from ten localities gather in 24 grades, from 80% to 104%. Moreover, if we can show that the extremes of variation of 3000 American shells from the three localities which offer the *least* variation are further removed than the extremes of the 3000 British shells taken at random, then our position is further strengthened. This we can do, for the combined amplitude of variation of 3000 British shells is 17, while the combined amplitude of variation of the three *least* variable American series is 19.

A Third Test of Variability.

Every one has doubtless observed the difference in the general proportions of the body of the child and the adult. In the former the head is relatively larger, the trunk longer, and the legs shorter. To use a conchological term, the child is more ventricose. Are the smaller shells, from the several

localities, of the same general proportions as the adults? If they are of different proportions, do they differ in a definite way? Is the difference greater in the American than in the British shells?

To answer these questions it will be expedient to divide each complement of shells into five groups: one group including all shells which are less than 15 mm. in height; a second, a third, and a fourth group containing shells ranging respectively from 16 to 17, 18 to 19, 20 to 21 mm. in height; and a fifth group containing all over 21 mm. in height.

On Chart I it will be noted that there are respectively 114, 308, 319, 183, 76 shells in the several groups, and the distribution of the 1000 shells in the several groups indicates, other things being equal, the general size of the shells of a particular locality. Thus, if the shells in a particular locality are small, the lower groups will contain a larger number. If the general proportions of the shell remain the same through the successive stages from infantilism to senility, the curves of distribution of these several groups will lie directly over each other, and a line drawn through their ideal means will be vertical. If the proportions of the shells vary with age, then the line connecting the five ideal means (the curve of growth) will bend, and its trend and its irregularity will indicate the amount of change.

The younger shells from Tenby, Wales (Chart I), are slightly more ventricose than the adults, the curve of growth tending towards the right at the lower part of its course and towards the left at the upper part. The amount of variation, however, is only 1.1 degree ($91.5 - 90.4 = 1.1$). Even less variation is exhibited by the South Kincardineshire shells, while the curve of growth for the Humber District is almost a straight line, varying only .3 of 1%. In all three cases the old shells are less ventricose.

The course of the curve of growth on the first American chart (Chart IV) indicates that the American shells, at least from this locality, are, in this third respect, more variable. Though the older shells still exhibit greater elongation, the curve of growth covers 2.9 degrees, an amplitude more than twice as great as that covered by the *most variable* British

curve.   The curve of growth for Casco Bay is also more
variable, as it is for Beverly, Nahant, Plymouth, Seaconnet,
and, indeed, for all the American localities, without a single
exception.

The Fourth Test of Variability.

If we weigh the empty shells of 200 snails from Tenby,
Wales, all of approximately the same height (18 to 19 mm.), we
will find that they vary in weight from 1.4 grams to 2.5 grams;
i.e., the index of their amplitude of variation according to weight
is 1.1.   Those from South Kincardineshire and those from the
Humber District vary from 1.5 grams to 2.4 grams, the index
of variation being in both cases .9.   The curves of distribution,
according to weight, of the shells from the three British local-
ities are represented on Chart XIV by dotted lines, and similar
curves of weight for nine American localities are represented
by entire lines.   (The shells from the St. Croix River were not
weighed, as they were cleaned in a manner different from those
from other localities, and their introduction would lead to
error.)

In every case it will be noted that the length of the base
line of the curve of the American shells, even when there are
less than 200 (indicated by the figures at the left of the chart),
is equal to or exceeds in length the base line of the curve of the
most variable British shells.   The index of the amplitude of varia-
tion according to weight of the most variable British shells is
11, while the amplitude of five of the least variable American
shells is also 11; four American localities, however, have an
increased amplitude; *viz.*, 12.   The *least* amount of variation
among the British shells is 9 ; the least among the American
is 11.

The lightest American shell weighs 1 gram ; the lightest
British shell, 1.4 gram.   The heaviest American shell weighs
2.6 grams; the heaviest British, but 2.5 grams.   The lightest
and heaviest shells are American.

A Fifth Test of Variability.

It will be noted on Chart XIV [1] that the three British curves lie directly under each other. The curves are not only alike in their general configuration, but the ideal weights, as indicated by the vertical curve, are approximately the same. Among the American curves it will be noted that there is more variation both in the contour of the curves and, what is more important, in the vertical curve of ideal means. No manipulation of data or combination of three American localities can be made which will not give an amplitude of variation according to weight which is greater than any combination of the three series of British shells.

A Sixth Test of Variability.

It is, unfortunately, impracticable to express variations in color either by curves or mathematical formulae. Color averages are uncertain and the estimation of extremes difficult.

The bands of color of the British shells are generally clearly defined throughout their entire length, and give a distinct cast to the British shells, whatever their age. The limits of the bands and the edges of the lines are much more irregular and indefinite in the American forms, and the amount of pigment and its distribution in the individual shells is more variable. Thus, the American shells have a mottled appearance and a suggestion of indefiniteness of color that the British shells seldom possess.

[1] On this chart the Roman numerals, at the right, indicate the localities from which the shells are collected, and the Arabic numerals, at the left, indicate the number of specimens used in the plotting of each curve. The lower curve is based on 200 specimens from Tenby, Chart I ; the upper curve is based on 183 specimens from Beverly, Chart VI. In the middle of each horizontal curve is a number which indicates the mean weight. The shells from Tenby have a mean weight of 1.86 grams ; those from Beverly have a mean weight of 1.43 grams. A vertical curve connects the several mean points, and since it bends to the left, as it ascends, it indicates that the American shells are lighter than the European. The very irregular curve of relative buiks, or displacements, drawn at the right, is intended to show the lack of dependence of the factor of weight upon bulk.

General Questions.

The questions naturally arise: (1) Are the American shells, together with their excessive variability, tending toward the establishment of a new type? (2) Do they offer another example of the principle of "mutation"? or, (3) Do the variations arrange themselves symmetrically around the Old World type?

An examination of the several charts will show that:

(a) While the British shells have an average stature of 89.6 $\left(\dfrac{90.9 + 87.5 + 90.5}{3} = 89.6\right)$, the average stature of the American shells is 91,

$\left(\dfrac{91.3 + 92.5 + 90.6 + 92.2 + 90.0 + 89.7 + 89.2 + 90.8 + 91.1 + 92.6}{10} = 91\right)$.

The American shells are thus 1.4% longer in proportion to their breadth than the British.

(b) While the British shells of 18 to 19 mm. in height have an average weight of 1.85 grams, the American shells of the same height have an average weight of 1.68 grams. The American shells are thus .1 lighter than the British.

(c) While the British shells of 18 to 19 mm. in height have an average displacement of 2.67 cc. $\left(\dfrac{2.75 + 2.50 + 2.77}{3} = 2.67\right)$ — see curve at right of Chart XIV — the American shells of the same height, even though they are lighter in average weight, are relatively and actually larger, for their average displacement is 2.80 cc. (Chart XIV).

$\left(\dfrac{2.75 + 2.71 + 3.05 + 2.62 + 3.05 + 2.55 + 2.62 + 3.05 + 2.82}{9} = 2.80\right)$

The shells from the Warren River, though extremely light, having an average weight of only 1.48 grams, are nevertheless quite as bulky, that is, their displacement is quite as great as that of the heaviest American shells of equal length.

(d) While the color markings of the British shells are laid down with precision, the color markings of the American shells are indefinite and give a characteristic mottled appearance.

Conclusion.

We may then conclude that the periwinkle, subjected to a new environment, and presumably emancipated from many of the restraining influences of natural selection, has become in any and in all American localities:

I and II. More variable in its stature.

III. More variable in its course of growth.

IV. More variable in weight.

V. More variable in bulk.

VI. More variable in the limitations and boundaries of the color patterns.

While presenting these extremes of variation, the American type of *Littorina littorea*, when compared with the European type, is more elongated, lighter in weight, more bulky, and the color markings are less pronounced.

These results are in harmony with and fully corroborative of the conclusions reached from the statistical study of the sparrow's egg.

BROWN UNIVERSITY, PROVIDENCE, R. I.
　　　September 10, 1897.

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CHART I. 1,000 LITTORINA LITTOREA. TENBY, WALES.

22-mm.

90.4 — 76

20-21 mm.

90.4 — 183

18-19 mm.

91.5 — 318

16-17 mm.

91.0 — 308

-15 mm.

174 — 169

155 — 114

91.2

120

101

77

56

45

38

25

22

8

4 4

90.9

1

80 81 82 83 84 85 86 87 88 89 90 91 92 93 94 95 96 97 98 99 100 101 102 103 104 105 106

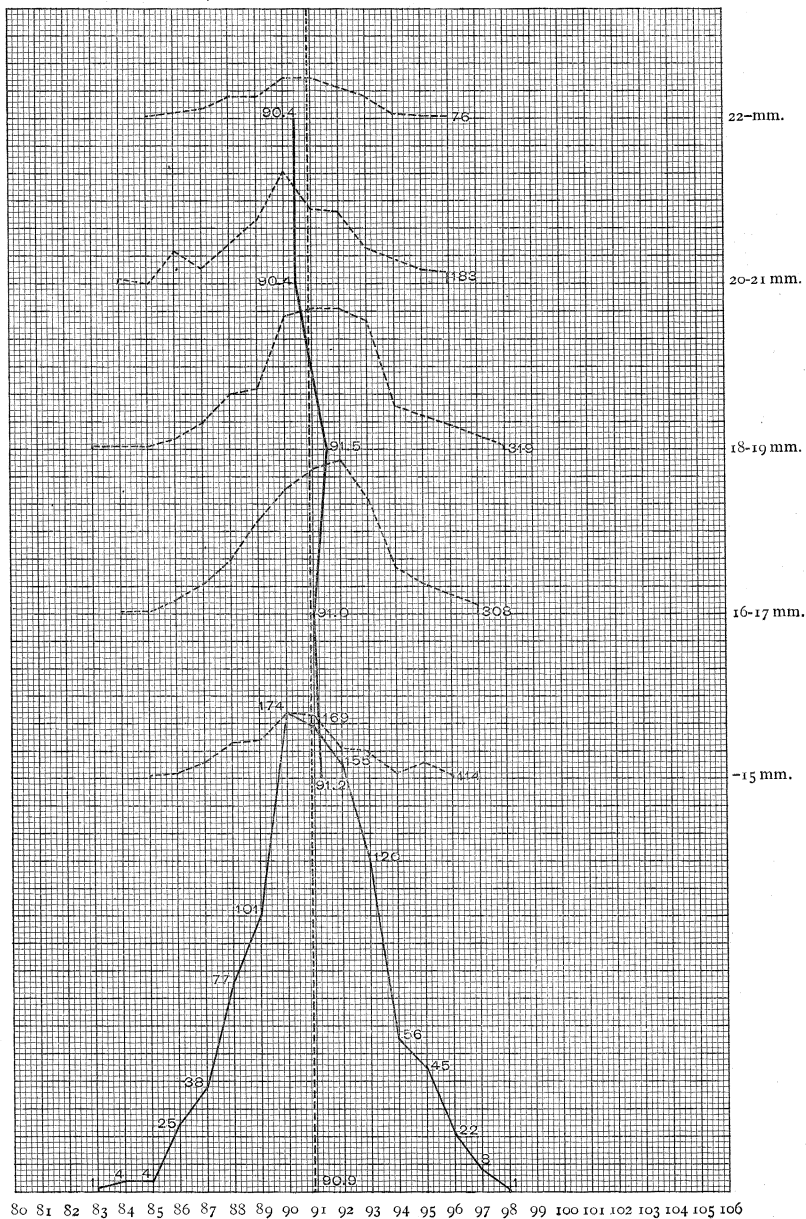CHART II. 1,000 LITTORINA LITTOREA. So. KINCARDINESHIRE.

CHART II. 1,000 LITTORINA LITTOREA. So. KINCARDINESHIRE.
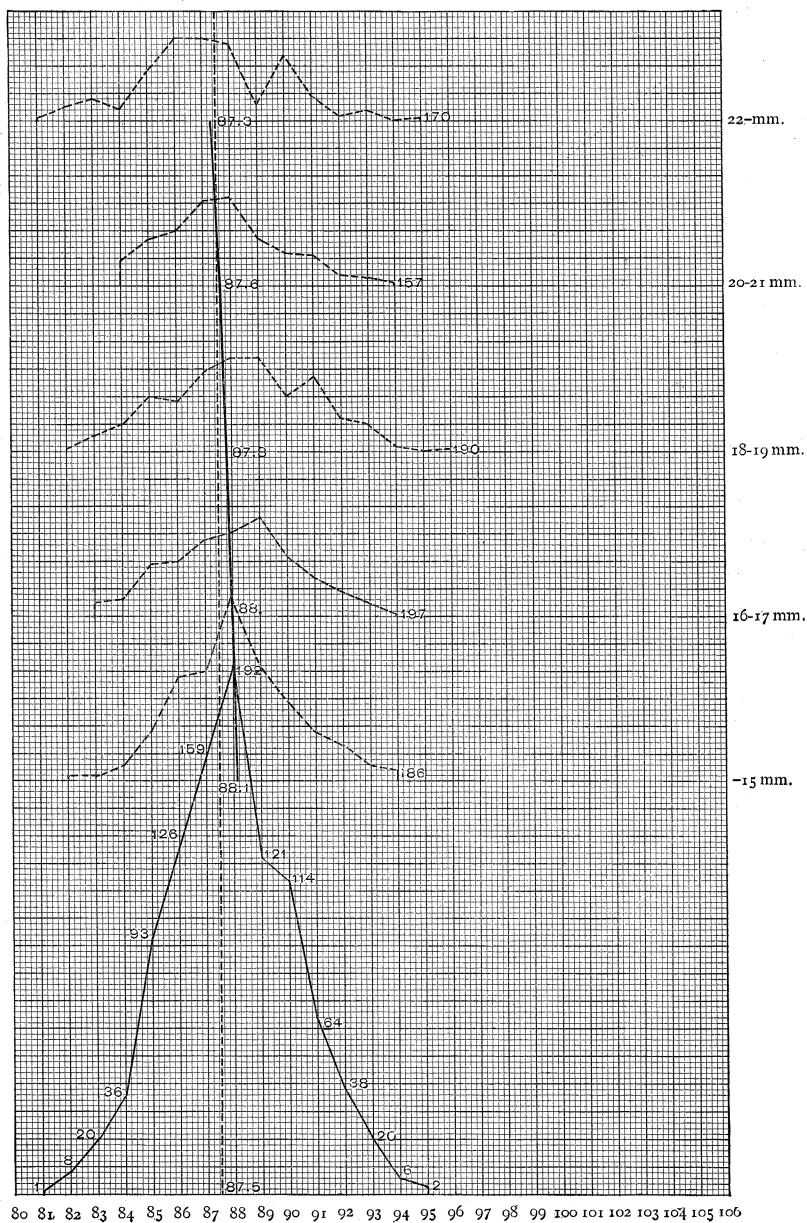
CHART III. 1,000 LITTORINA LITTOREA. HUMBER DISTRICT.

CHART III. 1,000 LITTORINA LITTOREA. HUMBER DISTRICT.

90.3   92   22-mm.

90.6   215   20-21 mm.

90.5   346   18-19 mm.

90.5   254   16-17 mm.

190
161
90.5   63   15 mm.
                133
132
101
                    90
61
                        49
                    36
28
2   14
90.5   2

80 81 82 83 84 85 86 87 88 89 90 91 92 93 94 95 96 97 98 99 100 101 102 103 104 105 106
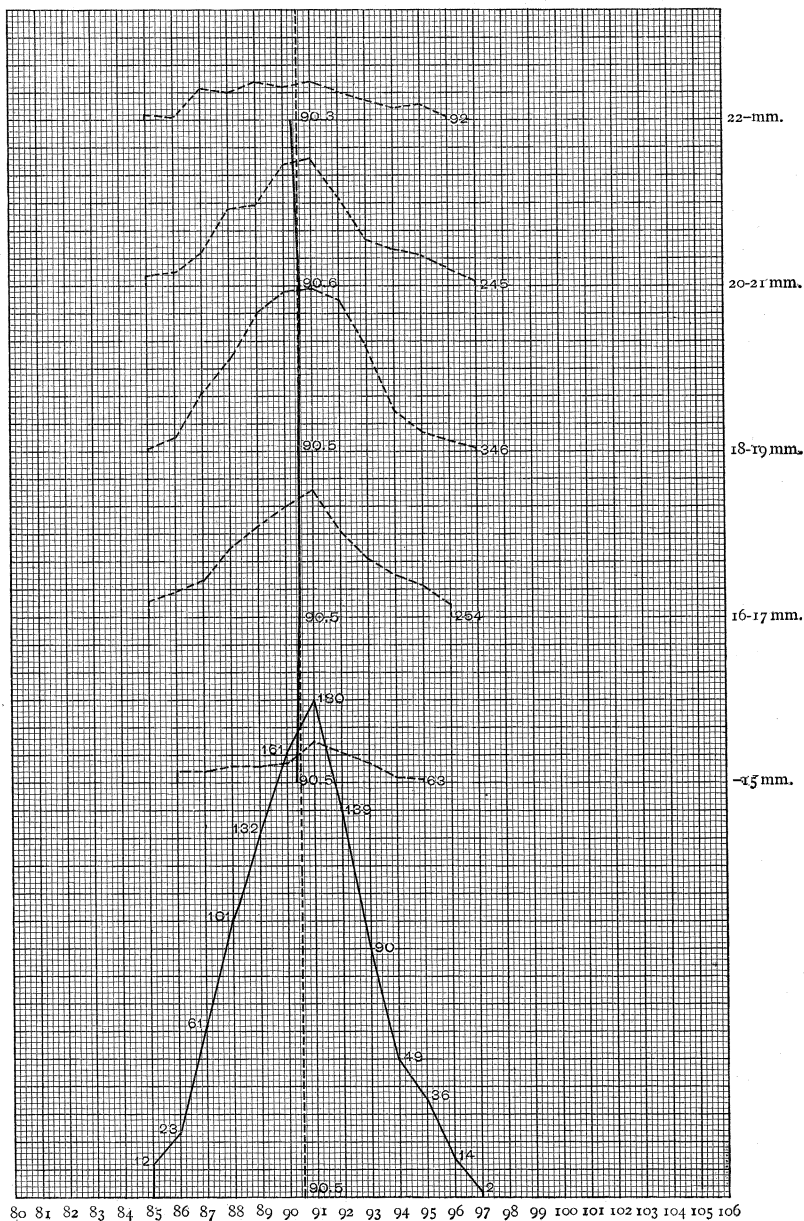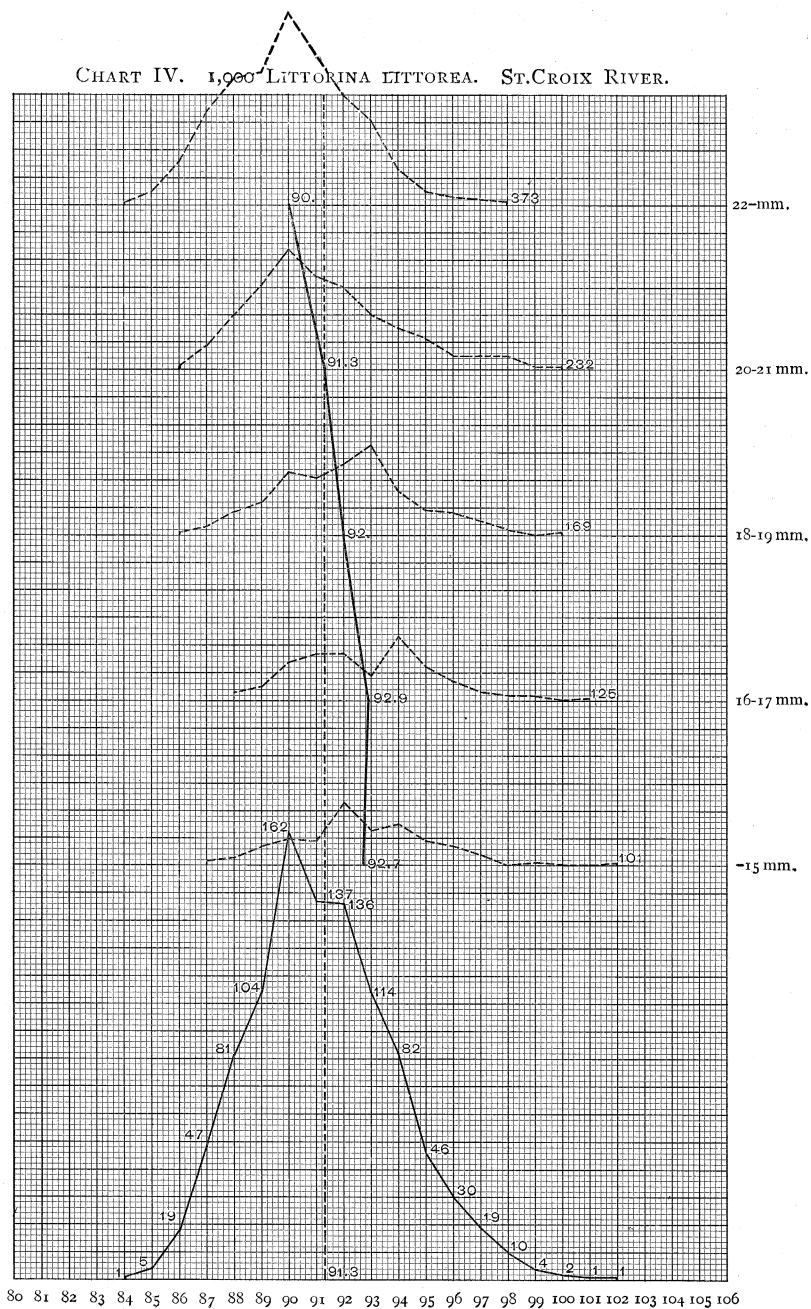
CHART IV. 1,000 Littorina littorea. St. Croix River.

CHART V. 1,000 LITTORINA LITTOREA. CASCO BAY, ME.
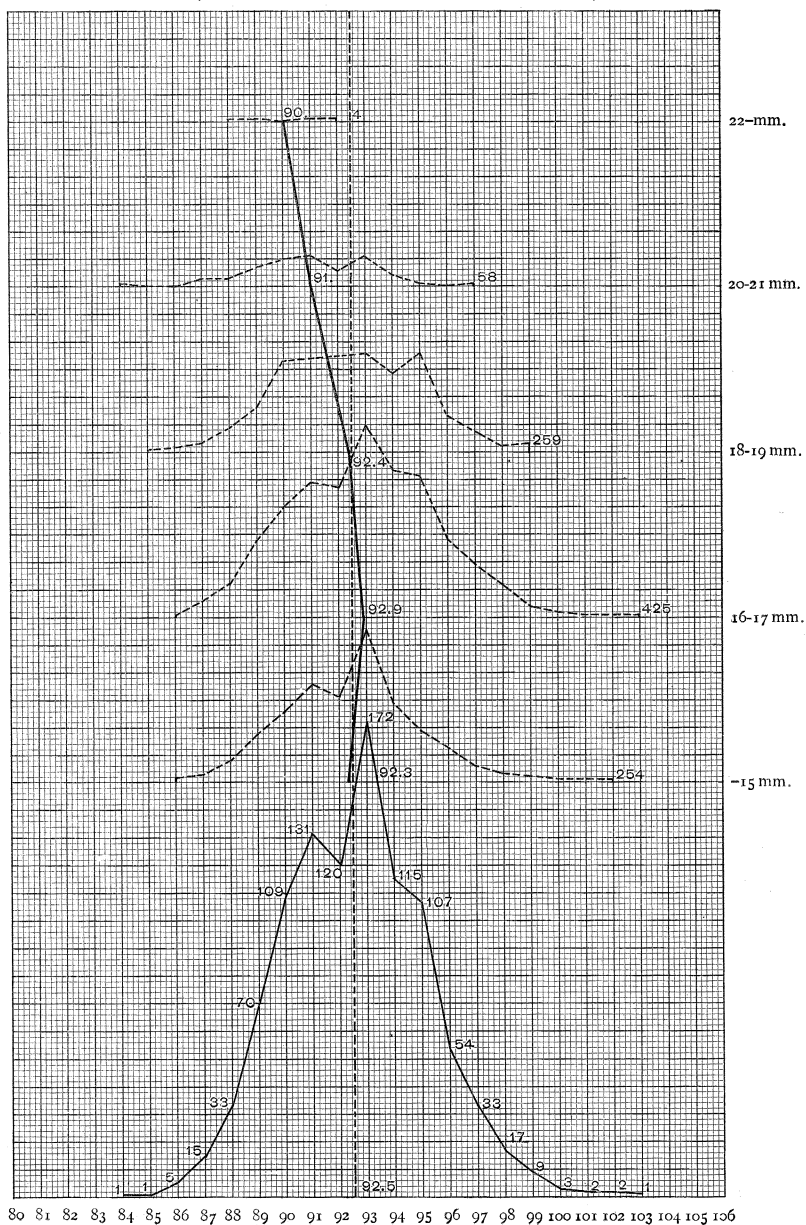
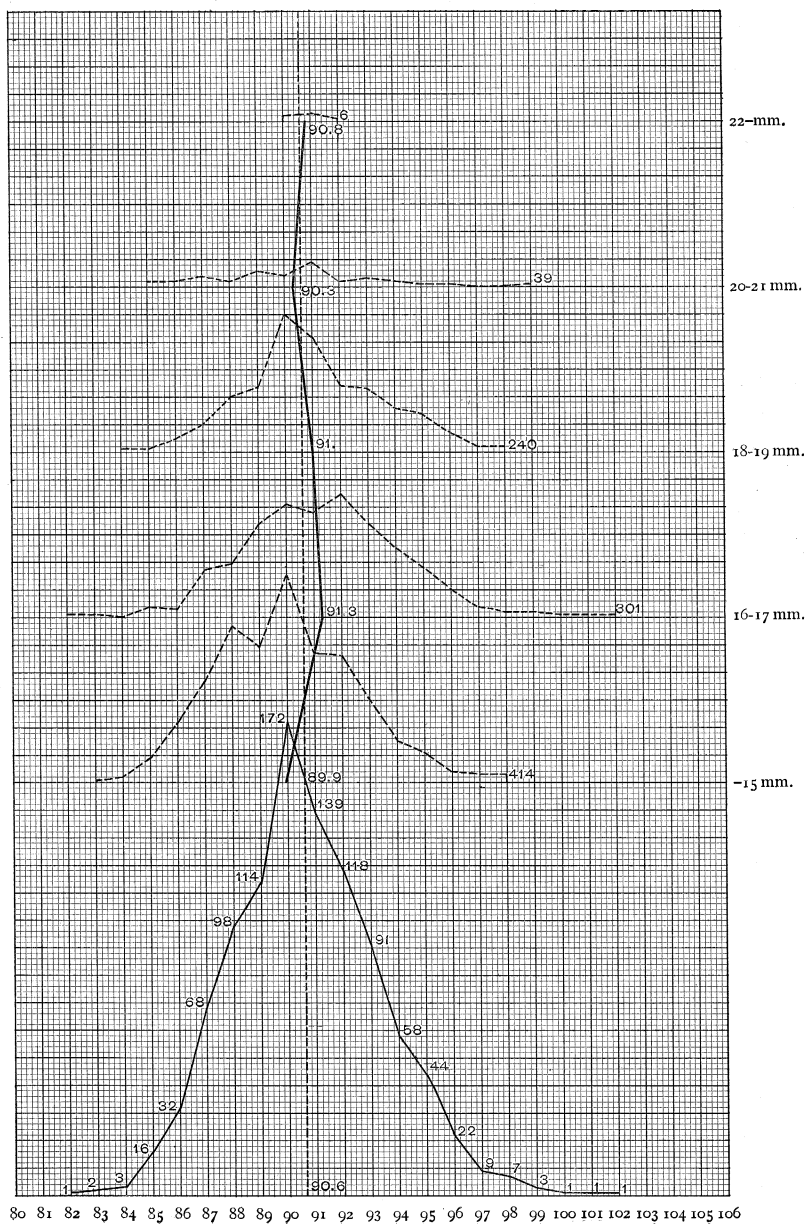CHART VI. 1,000 LITTORINA LITTOREA. BEVERLY, MASS.

6
90.8

22–mm.

39

90.3

20-21 mm.

91.

240

18-19 mm.

91.3

301

16-17 mm.

172

89.9

414

–15 mm.

139

118

114

98

91

68

58

44

32

22

16

9   7

1   2   3   90.6   3   1   1   1

80 81 82 83 84 85 86 87 88 89 90 91 92 93 94 95 96 97 98 99 100 101 102 103 104 105 106

CHART VII. 1,000 LITTORINA LITTOREA. NAHANT, MASS.

91.3   127   22-mm.

92.5   273   20-21 mm.

92.9   200   18-19 mm.

92.2   200   16-17 mm.

91.7   200   -15 mm.

137
126
118
112
104
90
64   67
50
30   33
19   17
3   5   8   10
92.2   6   2   1

80 81 82 83 84 85 86 87 88 89 90 91 92 93 94 95 96 97 98 99 100 101 102 103 104 105 106
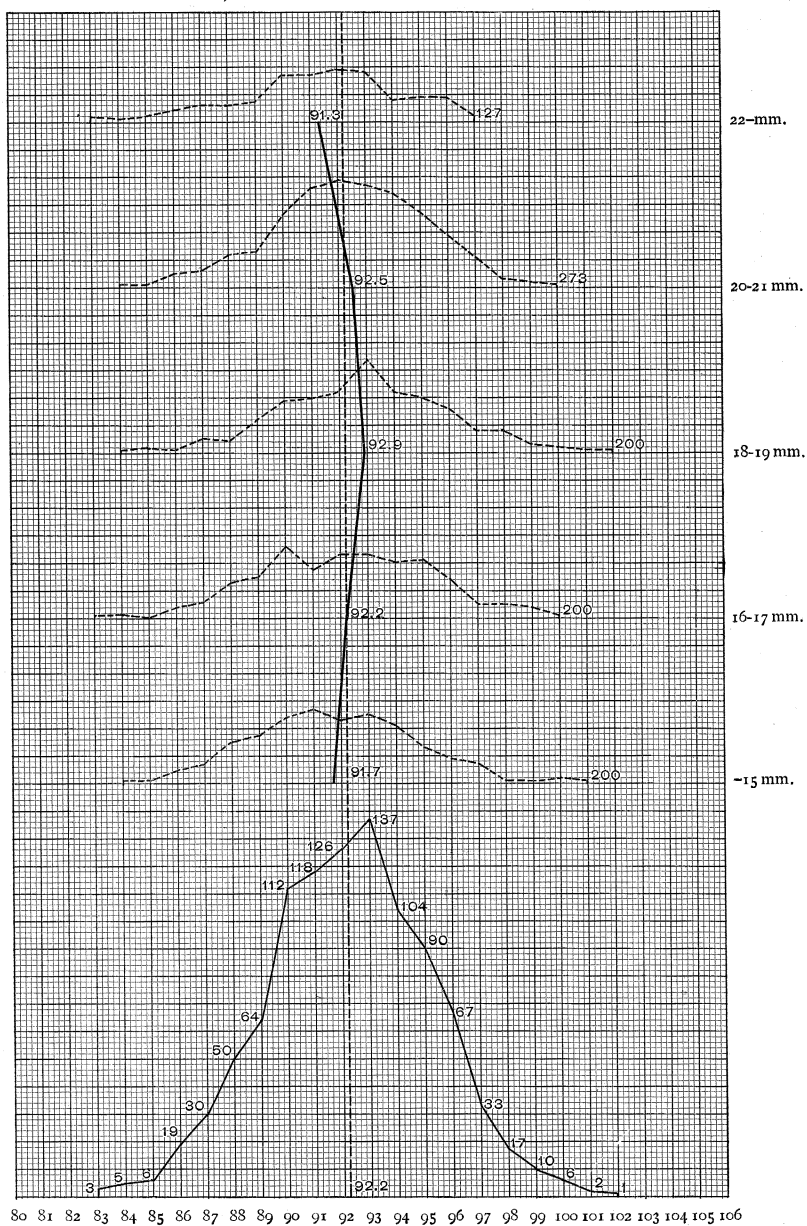
CHART VIII.   1,000 LITTORINA LITTOREA.   PLYMOUTH, MASS.
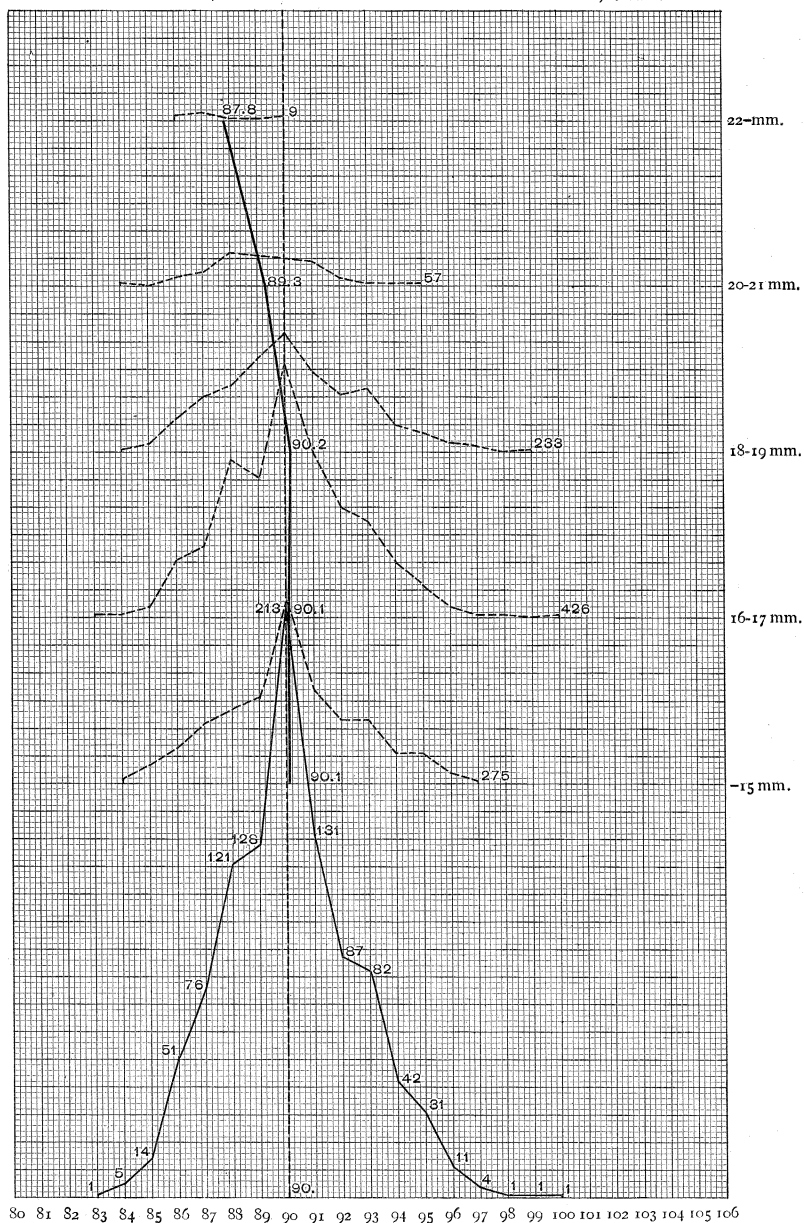
CHART IX. 1,000 LITTORINA LITTOREA. SEACONNET, R.I.

91.5   200   22-mm.

91.3   188   20-21 mm.

89.2   202   18-19 mm.

88.6   181   16-17 mm.

88.2   229   -15 mm.

139 143

121

111

92   96

69   75

44

30   27

17   14

1 2 2 7   89.7   5 2 2 1

80 81 82 83 84 85 86 87 88 89 90 91 92 93 94 95 96 97 98 99 100 101 102 103 104 105 106
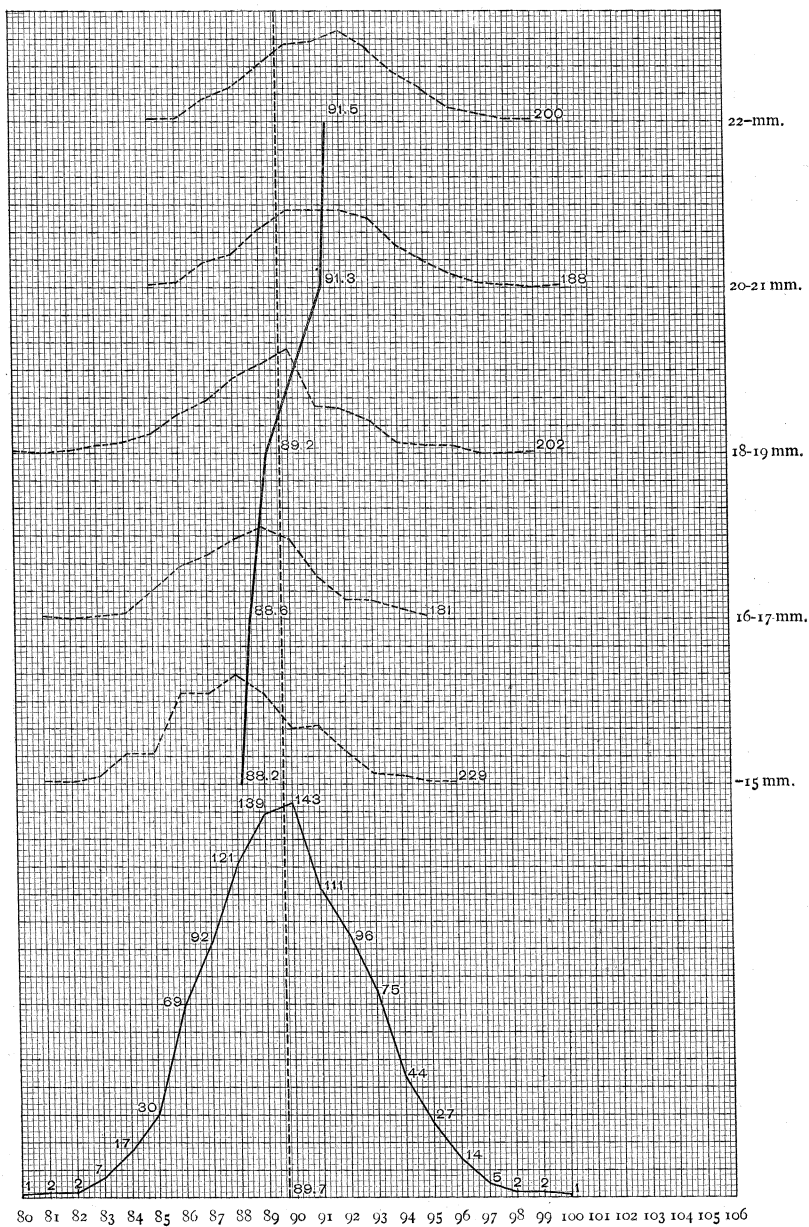
CHART X. 1,000 LITTORINA LITTOREA. NEWPORT, R.I.
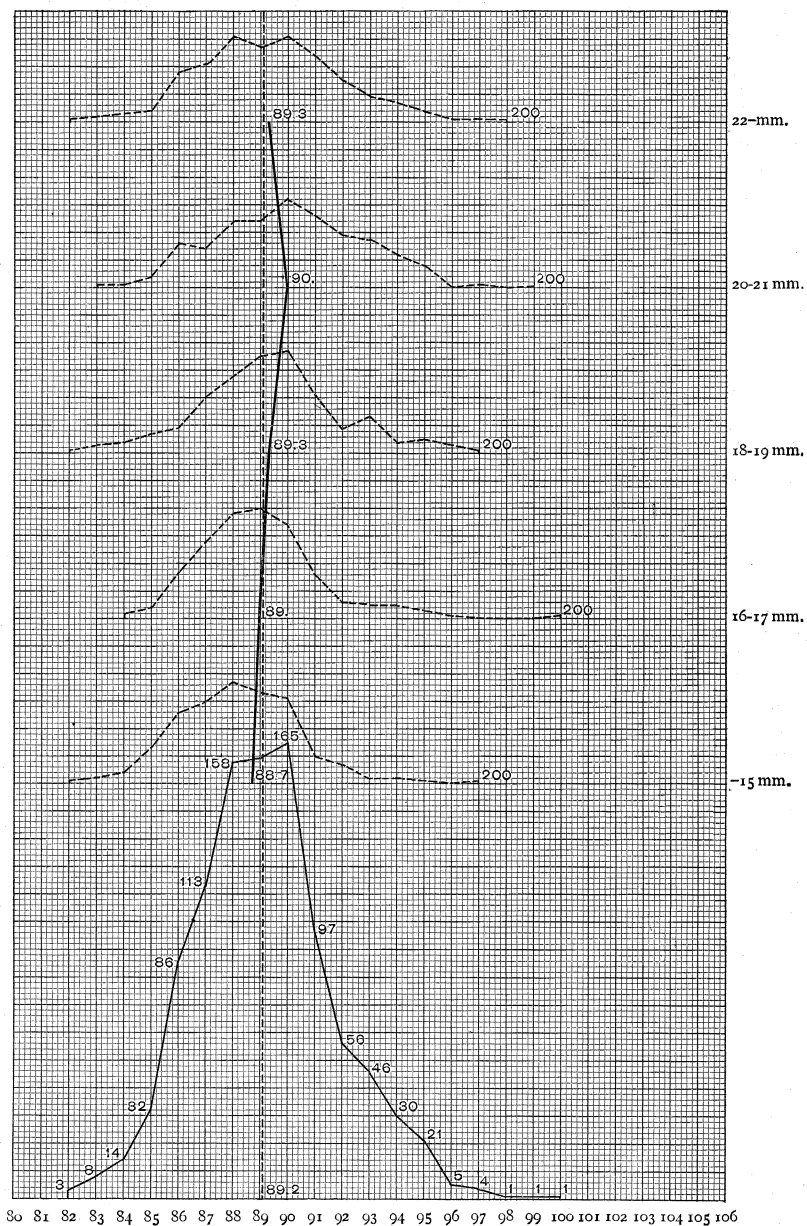
CHART XI. 1,000 LITTORINA LITTOREA. BRISTOL, R.I. (SHINGLE)
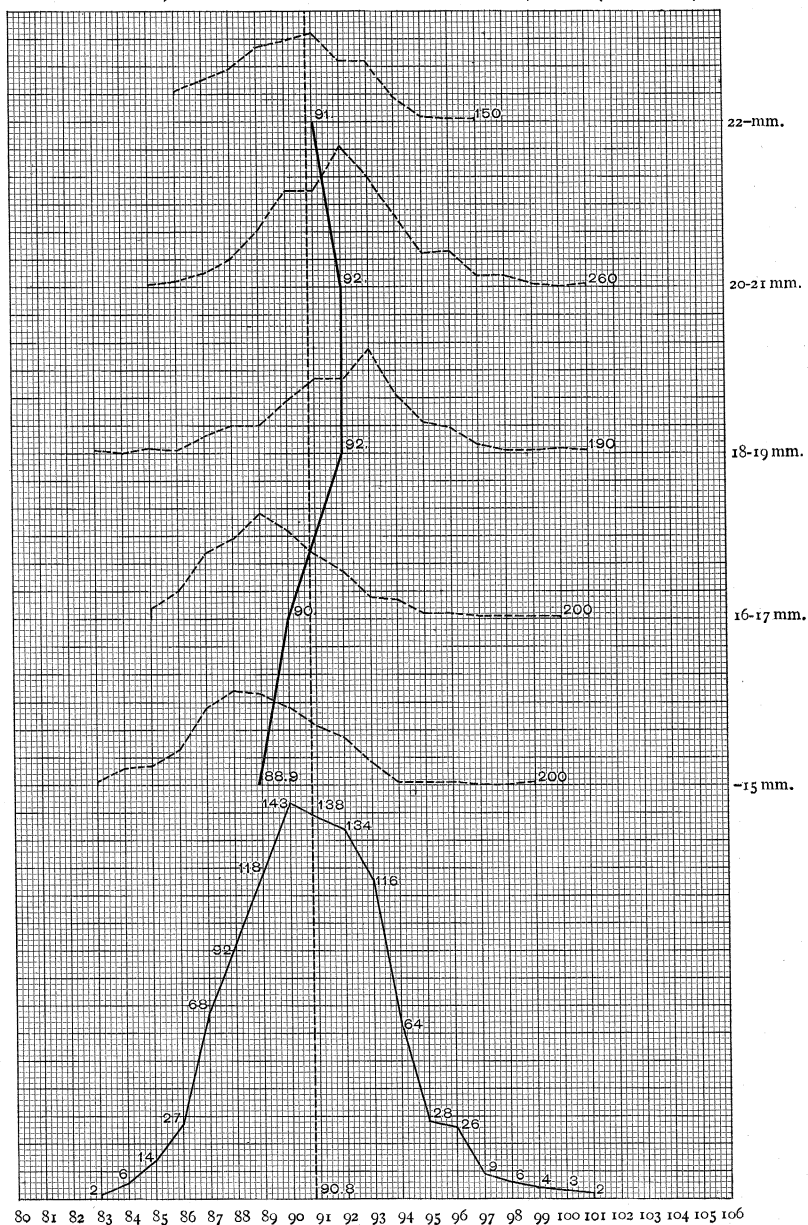
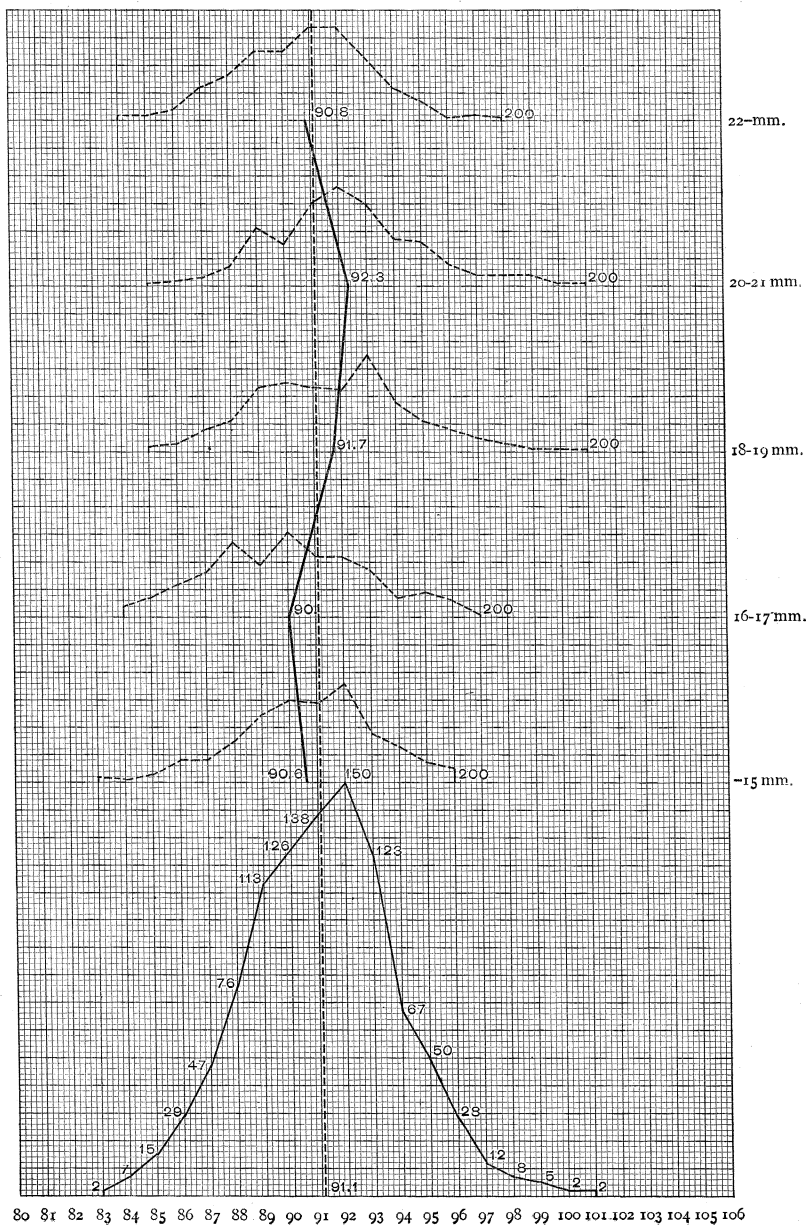CHART XII. 1,000 LITTORINA LITTOREA. BRISTOL, R. I. (SAND)

90.8   200   22–mm.

92.3   200   20-21 mm.

91.7   200   18-19 mm.

90.1   200   16-17 mm.

90.8   150   200   –15 mm.

138

126   123

113

76

67

50

47

29   29

15   12

8

2   91.1   5   2   2

80 81 82 83 84 85 86 87 88 89 90 91 92 93 94 95 96 97 98 99 100 101 102 103 104 105 106

CHART XIII. 1,000 LITTORINA LITTOREA. WARREN RIVER, R.I.

22-mm.

20-21 mm

18-19 mm.

16-17 mm.

-15 mm.

80 81 82 83 84 85 86 87 88 89 90 91 92 93 94 95 96 97 98 99 100 101 102 103 104 105 106